

A REVIEW OF THE GENUS *TACHYGONUS* (COLEOPTERA: CURCULIONIDAE) NORTH OF MEXICO

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Abstract.—Examination of types of North American *Tachygonus* shows that there are five valid species that occur north of Mexico: *T. lecontei* on oaks, *T. tardipes* on elm, *T. centralis* on locust (*Robinia*), *T. rhombus* on *Coursetia*, and *T. fulvipes* on *Berchemia*. Characters and placement of the genus are discussed. A key to North American species is presented as well as diagnoses and figures; five new synonymies are proposed. Variation in color patterns of *T. rhombus* and *tardipes* is documented, and that in *T. lecontei* is analyzed geographically. Arizona populations on oak, assigned here to *T. lecontei* may represent more than one distinct species, but require additional collecting and perhaps biological studies to determine species limits.

Key Words: Biogeography, host plants, intraspecific variation, leaf-miners

The weevil genus *Tachygonus* Schoenherr is widely distributed in the New World, occurring from Canada to Argentina. Members of the genus are unusual morphologically in being dorsoventrally flattened, having enlarged hind legs which articulate primarily in the plane of the body rather than perpendicular to it, and possessing a very short first antennal segment. At least part of their unusual form is related to their larval ecology as leaf-miners. Unfortunately, little has been published on the biology of the genus other than a life history of one Brazilian species (Kogan 1963) and the adult behavior of a Panamanian species in the closely related genus *Tachygonidius* (Aiello and Vogt 1986; review in Hespenheide 1991). Similarly, the ecology of North American species is largely unknown, other than for *T. lecontei* or mention of host plants for other species (see below).

The genus *Tachygonus* was first proposed by Schoenherr for the North American species *T. lecontei* in 1833. LeConte (1868, 1876) described three additional species and

Casey (1897) named three more forms in his revision; two other names have been proposed subsequently (Blatchley 1920, 1922). The existence of several apparently unique types and the discovery of extensive variation in three North American species indicated a need for a review of the genus. From the study of these types and other material, I conclude here that the fauna of America north of Mexico consists of five species and that five other names are synonyms, although further study is needed of southwestern populations assigned here to *T. lecontei*.

Tachygonus Schoenherr

As mentioned above, the genus *Tachygonus* is characterized by the short scape and non-geniculate antennae and the unusual hind legs, making its members "among the strangest insects of the family" (LeConte 1876). In most recent catalogues (O'Brien and Wibmer 1982, Klima 1936) and treatments (Blatchley & Leng 1916) the genus is given its own subfamily, together with one

other small New World segregate (*Tachygonidius*, Champion 1906) and with two Old World genera that are probably not related. When the large number of undescribed Neotropical species are studied, additional genera may well be recognized. In addition to striking modifications of the hind femora (Champion 1906: 131), I have found that species of *Tachygonus* differ in the structure of the mesosternum and in the presence or absence of a visible scutellum (see below), which are characters often used to separate genera, for example in the Zygotinae.

The relationships and placement of *Tachygonus* are uncertain. Although currently treated as its own subfamily, it has also been treated as a tribe (LeConte 1876, Casey 1897) or even as a family (Pierce 1916). It seems likely that its morphology is highly derived as a consequence of its ecology. Several authors have suggested a connection with the Zygotinae: LeConte (1876) noted the large eyes and very narrow front; Casey (1897), the 7-jointed funicle and the large, curved tibial spine; and Champion (1906), the pectinate setae shared with *Philides*. Champion (1906) placed the genus immediately after *Philides* and the "Zygotina." *Tachygonus* also shares an exposed pygidium and enlarged simple pale setae along the apical margin of the elytral suture with *Philides* and *Philinna*, although placement of these genera in the Zygotinae is uncertain (Champion 1906: 129). Several genera in the Zygotinae possess enlarged, elongate posterior legs, including arcuate, flattened tibiae (*Mnemyne*, *Paramnemyne*, *Paramnemyne*, etc.), although none of these are very similar to *Tachygonus* in specific details.

Within the genus, species have typically been separated by characters from the structure of the posterior legs (LeConte 1876, Casey 1897), especially their size and shape, the number and size and position of the teeth on the femora, and the shape of the tibiae. The overall shape and ground color and the pattern of setae have also been used,

but these prove to be quite variable and difficult to interpret unless large series of specimens are available. In addition to the mesosternum and scutellum mentioned above, I have also found that species differ in the size and shape of the tarsi. North American species of *Tachygonus* can be separated by the following key. The five species are then considered in turn.

KEY TO NORTH AMERICAN *TACHYGONUS*

1. Mesosternum excavate and laterally carinate for receiving tip of rostrum; elytra black; pectinate setae of elytral disc bicolored, white and fulvous; legs bicolored; scutellum inconspicuous; Arizona, Mexico to Panama *rhombus* Casey
- Mesosternum transverse between middle coxae; elytra black, reddish or variegated; pectinate setae of elytra usually white; legs uni- or bicolored; scutellum conspicuous or not 2
2. Hind tibiae strongly curved, flattened, usually sharply angulate on external margin; erect tufts of dark setae on disc of pronotum on both sides of midline on basal half; erect tufts of white setae on elytral disk at apical $\frac{3}{4}$; scutellum conspicuous; length to tip of elytra usually greater than 2.5 mm; hosts: *Quercus* spp.; eastern United States to Guatemala *lecontei* Gyll.
- Hind tibiae straight or only slightly curved, not conspicuously flattened or angulate on external margin; small patches of semi-erect white setae at posterior angles of pronotum; semi-erect patches of white setae on elytra usually only along suture behind scutellum; scutellum conspicuous or not; length usually less than 2.5 mm 3
3. Elytra bicolored, yellowish and black; pectinate setae on elytra usually in several conspicuous patches; hind femora long, slender, not noticeably swollen, with three long slender spines on inner margin; scutellum conspicuous; host: elm *tardipes* LeConte
- Elytra black; pectinate setae on elytra in conspicuous patches only along suture behind scutellum; hind femora short, swollen, with few short teeth on inner margin; scutellum inconspicuous 4
4. Rostrum and legs all black; third tarsal joint scarcely wider than second; all elytral intervals similar; length usually greater than 2.1 mm; host: *Robinia* spp.; southwestern states
- *centralis* LeConte
- Apex of rostrum and at least fore tibiae yellow or pale; third tarsal joint conspicuously wider

than second; even elytral intervals elevated, at least at base; length usually less than 2.1 mm; Gulf states*fulvipes* LeConte

Tachygonus rhombus Casey, 1897: 681.
Tachygonus tardipes LeConte, 1884, not LeConte, 1876.

Form rhomboid, more narrowly attenuate in front than behind. Black, except antennae, fore and middle legs, basal half of hind femora yellowish- to brownish-orange; semi-erect white pectinate setae in small tufts at posterior angles of pronotum, on scutellum, and in spot on first elytral interval behind scutellum; recumbent white pectinate setae scattered on elytra, dense on base of rostrum, sides of pronotum, on epimera and episterna, somewhat sparser on ventral surface and basal half of hind femora; yellow-orange pectinate setae in spot along suture of elytra behind scutellum, more or less scattered on elytra, especially at base; simple erect white setae on pygidium and basal half of hind femora; coarse simple erect dark setae on pronotum, elytra, distal and hind tibiae. Figure 3.

Pronotum rather sparsely punctate, shining. Elytra coarsely punctate, intervals raised, even ones somewhat more strongly so. Mesosternum declivous with well-defined longitudinal groove for receiving tip of rostrum, with smooth, narrow channel in middle and margins on outer edge. Abdomen more or less uniformly punctate, more sparsely so in middle of segment 2. Hind femora relatively short, arcuately curved at base, moderately swollen beyond middle, with two acute teeth, inner one at distal $\frac{3}{4}$ and longer, outer one shorter, between inner tooth and middle; hind tibiae more or less terete and straight, slightly twisted outward at tip; segment 3 of tarsi equal in width to segment 2.

Distribution: Arizona, Mexico (Guerrero, Morelos, Oaxaca, Quintana Roo, Tamaulipas); Honduras (Copan); Costa Rica (Guanacaste); Panama (Panama).

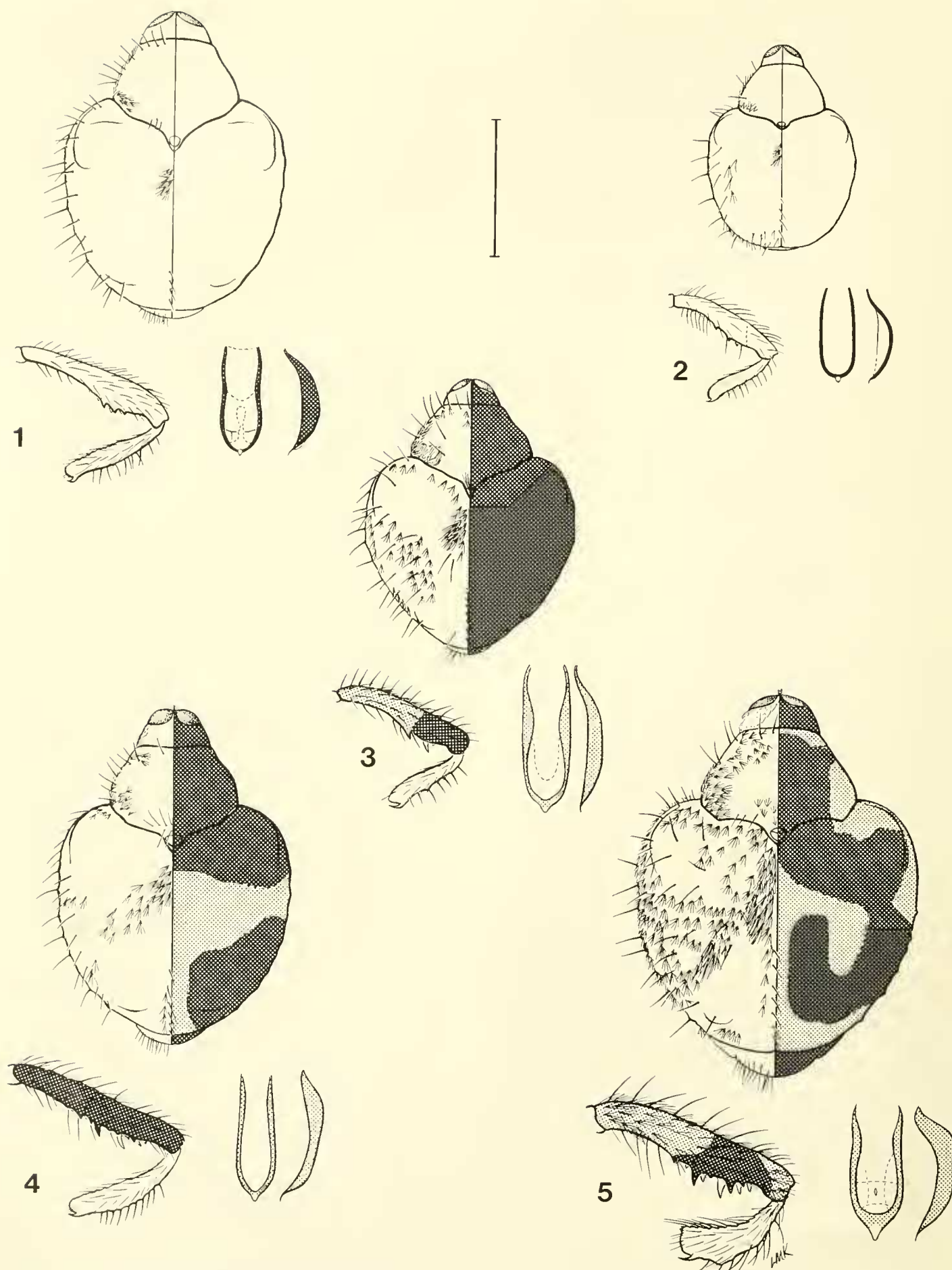
Adult host: *Coursetia microphylla* Gray (Fabaceae).

Discussion: As treated here, this species is rather variable, primarily in the density of pectinate setae on the disc of the elytra other than the post-scutellar tufts. The structure of the mesosternum has not been mentioned in previous publications on this or any other species of *Tachygonus*. In most members of the genus the mesosternum is transverse and essentially unmodified except for surface sculpture. It is modified in *T. rhombus* and about 11 other of about 60 species known to me from North and Central America, including the described forms *T. caseyi* Champion, *T. flavisetis* Champion, *T. semirufus* Champion, and *T. gowdeyi* Marshall. The inconspicuous scutellum is shared with *T. centralis* and *T. fulvipes* among North American species as well as with *T. caseyi*, *T. flavisetis* and *T. gowdeyi*.

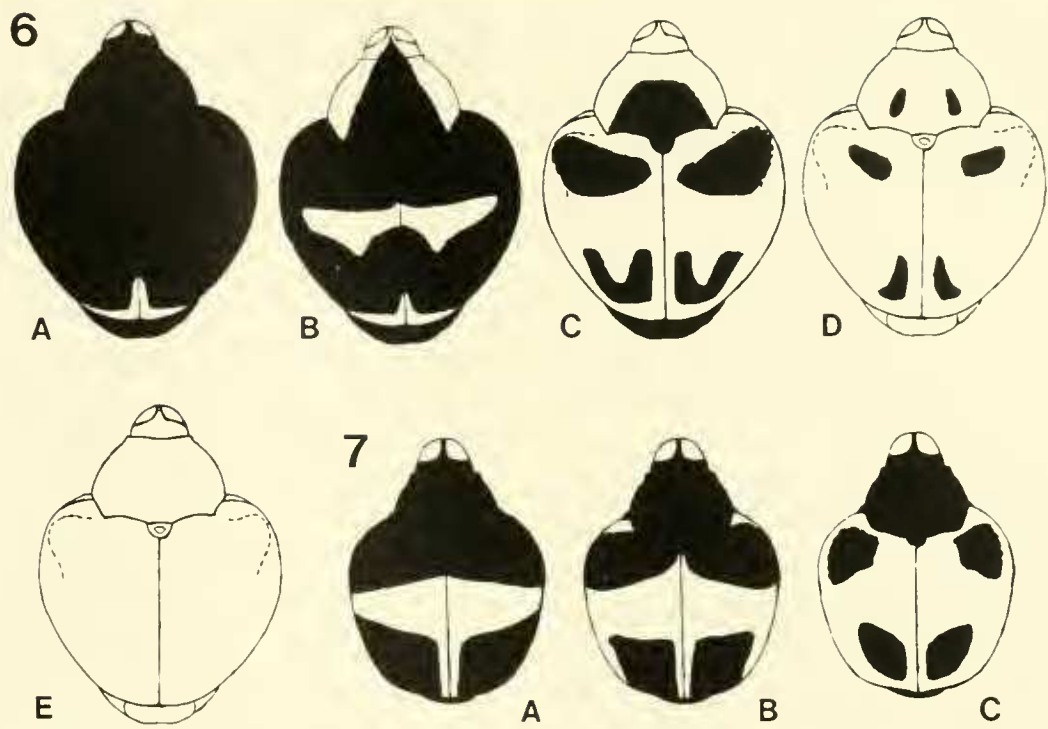
Although collected in numbers in Arizona by Morrison (Champion 1906, Casey 1897), there are only three recent collections, all from Tucson or nearby Sabino Canyon in the Santa Catalina Mountains, in one case from *Coursetia*. Two specimens in the U.S. National Museum are labelled "Cal.," but no other specimens are known from California.

Tachygonus lecontei Gyllenhal, in Schoenherr, 1833: 312.
T. horridus Chevrolat, 1835: pl. 38.
T. spinipes Casey, 1897: 680. NEW SYNONYMY.
T. bifasciculatus Champion, 1906: 135. NEW SYNONYMY.

Form ovoid-rhomboid, more narrowly attenuate in front, more rounded behind. Color very variable (Fig. 6; see discussion below), from the extreme of mostly dark reddish brown and only metasternum and abdomen black to mostly black except antennae, tip of rostrum, tips of elytra, fore and middle legs, and basal $\frac{1}{2}$ of hind femora pale to dark reddish brown; coarse simple erect dark setae in tuft on pronotum on either side of midline at basal $\frac{1}{3}$, elsewhere scattered on pronotum, elytra, distal half of



Figs. 1-5. North American species of *Tachygonus*; habitus, right posterior femur and tibia, genitalia in dorsal and lateral views; line = 1 mm for habitus and legs, = 0.5 mm for genitalia; in habitus left side shows pattern of setae, right side typical ground color of black and reddish brown (light shading). 1. *T. centralis*. 2. *T. fulvipes*. 3. *T. rhombus*. 4. *T. tardipes*. 5. *T. lecontei*.



Figs. 6–7. Variation in ground color. 6.(a–e) *Tachygonus lecontei*. 7.(a–c) *T. tardipes*.

hind femora and hind tibiae; semi-erect white pectinate setae in small dense tuft on elytra beyond middle and midway between suture and lateral margin, in larger diffuse tuft on elytra before middle and behind scutellum along interval 1, more or less dense white pectinate setae on front, sides of pronotum, epimera and episterna, lateral margins of metasternum and abdominal segments, along anterior margins and in transverse band across middle of elytra, and the basal 1/2 of posterior femora; simple erect white setae on pygidium and basal 1/2 of hind femora. Figure 5.

Pronotum densely punctate on disk, except for rectangular impunctate area along midline at middle, shining; scutellum conspicuous. Elytra coarsely punctate, intervals raised, humeri very prominent. Mesosternum vertical, transverse, glabrous. Abdomen relatively densely punctate except for transverse elliptical impunctate area along suture between segments 1 and 2. Hind femora relatively stout, somewhat swollen beyond middle, with inner and outer series of 3(–4) teeth, teeth stout, acute, slightly curved apically, outer teeth longer and series be-

ginning at middle of femora, inner beginning at 2/3 length, first in series longest; hind tibiae somewhat flattened, shallowly arcuate on inner margin, biangulate on outer margin, with narrower angle near apex, wider angle at basal 1/3, apex obliquely truncate inward; segment 3 of tarsi nearly 2 × wider than segment 2.

Distribution: Alabama, Arkansas, Arizona, District of Columbia, Florida, Georgia, Indiana, Louisiana, Maryland, Mississippi, New Jersey, New York, North Carolina, Ohio, South Carolina, Tennessee, Texas, Virginia; Mexico (Queretaro); Guatemala.

Larval hosts: *Quercus* spp.

Discussion: Examination of the types of all four names—those of *T. lecontei* and *horridus* from Stockholm, *spinipes* from the U.S. National Museum, and *bifasciculatus* from the British Museum—and study of the geographic variation in the color and setation pattern of the *Tachygonus* associated with oaks in North America (see below) shows both *spinipes* and *bifasciculatus* to fall within the range of variation of this widely distributed species, which argues against retaining the names. The name *spinipes* is

associated with the extreme form which has a combination of black ground color and sparse elytral setae. Because this extreme form turns up in widely separated geographic areas (Long Island, N.Y.; New Jersey; Maryland; Georgia; Arkansas; Ohio; Indiana) and because it occurs (in populations other than New York) mixed with other forms, there does not seem to be any special reason to retain the name even as a sub-specific epithet.

Although *T. lecontei* is the most widely distributed and frequently collected species of *Tachygonus*, there has been no published study of its life history. The leaf-mining insect faunas of oaks have been extensively studied ecologically (review in Hespenheide 1991), but have mentioned *T. lecontei* only in passing: Bultman and Faeth (1985) estimated densities on *Quercus falcata* Michx., *Q. hemisphaerica* Bartr. and *Q. nigra* L. in northern Florida to be relatively low (0.35–1.36/1000 leaves) among the 14 miners using the three oaks; Faeth and Simberloff (1981; their Table 1) estimated 2–3 generations/year and duration of the mining stages to be 30–60 d on these hosts at the same site.

Tachygonus tardipes LeConte, 1876: 266.
T. gracilipes Casey, 1897: 680. NEW SYNONYMY.

Form ovoid-rhomboid, rather irregularly attenuate in front, broadly rounded behind, elytra abruptly wider than pronotum. Color variable, mostly black or dark reddish brown, except yellow antennae, transverse band and more or less of rest of elytra (Fig. 7), fore and middle legs, and hind tarsi; tip of rostrum and hind tibiae light brown; semi-erect white pectinate setae on elytra in irregular patch interior to suture and behind scutellum, in small spots on disk, and on apical margins; recumbent white pectinate setae on sides of pronotum and metepisterna, sparsely on metasterna and abdominal segments 1–2, densely on posterior margin of segment 2; simple erect white setae on

pygidium and basal $\frac{1}{2}$ of hind femora; coarse simple erect dark or yellowish setae on pronotum, elytra, distal half of hind femora and hind tibiae. Figure 4.

Pronotum conspicuously constricted behind apex to form “collar,” noticeably convex from side, moderately punctate on disk, more sparsely so along midline at middle, shining; scutellum conspicuous. Elytra finely punctate, punctures separated by more than their diameters, intervals raised, even ones more strongly so. Mesosternum vertical, transverse, finely transversely rugose. Abdomen sparsely punctate on segments 1 and 2. Hind femora long, straight, scarcely swollen, with 2 long acute spines on inner side beyond middle and a third on outer side at middle; hind tibiae long, shallowly arcuate, especially on outer margin, somewhat flattened; segment 3 of tarsi nearly 2 × wider than segment 2.

Distribution: Indiana, Ohio, New York, Pennsylvania, Texas; Canada (Ontario).

Adult hosts: *Ulmus* spp.

Discussion: Examination of the types of both names and study of the variation among specimens at a single locality (Cincinnati, Ohio) shows that these names should be considered to refer to the same species. Variation occurs primarily in the proportion of black and yellow on the elytra (Fig. 7) and is similar to, albeit less extensive than the range of variation shown by *T. lecontei*. Adults are associated with elm (*Ulmus americana* L.) and the species seems most common in the upper Ohio River Valley. Although the type of *T. tardipes* is from Texas without locality and therefore apparently disjunct, there is a recent collection from Burleson County (R. H. Turnbow).

Tachygonus centralis LeConte, 1868: 55.
T. fulvipes var. *nigrescens* Blatchley 1922: 98. NEW SYNONYMY.

Form rhomboid, rather narrowly attenuate in front and behind, elytra abruptly wider than pronotum. Black, except antennae, tips of tibiae, and last two tarsal seg-

ments pale yellowish brown; semi-erect white pectinate setae in small tufts at posterior angles of pronotum, and in large spot along suture behind scutellum; recumbent white pectinate setae on sides of pronotum, metepisterna and sides of metasterna, and posterior corners of abdominal segment 2; simple erect white setae on pygidium and basal half of hind femora; coarse simple erect dark setae on pronotum, elytra, distal half of hind femora and hind tibiae. Figure 1.

Pronotum moderately densely punctate, shining; scutellum inconspicuous. Elytra coarsely punctate, punctures larger than intervals, intervals slightly raised. Mesosternum vertical, transverse, smooth. Abdomen coarsely, densely punctate. Hind femora slender at base, swollen at apical $\frac{2}{3}$, with 2–3 short, blunt teeth or tubercles; hind tibiae terete and nearly straight, slightly twisted outward at tip; segment 3 of tarsi only slightly wider than segment 2.

Distribution: Arizona, Colorado, Illinois, Nebraska, New Mexico, Texas.

Adult host: *Robinia neomexicana* Gray (Fabaceae).

Discussion: Of 141 specimens examined in this study, all but 12 were collected in Arizona, where it occurs widely. Specimens from Nebraska (AMNH) and Texas (USNM) were without further locality data. Blatchley (1922) in the original description of his “variety” *nigrescens* suggested that it might prove to be conspecific with *centralis*. My examination of the type of *nigrescens* in the Field Museum confirmed his suspicion. The type of *nigrescens* is from Illinois, far from the next closest specimens from Nebraska. This species is relatively common on its host plants in Arizona, shrubs of the genus *Robinia*. LeConte (1868) records the type as occurring on a species of *Rhus* in Colorado, but the specimen labelled as the type in the Museum of Comparative Zoology also has a “N.M.” label; three other specimens associated with the type are unlabelled. The original description gives the length as “1.5 mm,” although the smallest

of the four specimens is 1.9 mm and the type is 2.3 mm. Because no other species of *Tachygonus* are known from the area, there is no confusion about the identity of *T. centralis*, but the typification deserves further study.

Tachygonus fulvipes LeConte, 1876: 266.

T. minutus Blatchley 1920: 263. NEW SYNONYMY.

Form ovoid, rather narrowly attenuate in front, broadly rounded behind, elytra abruptly wider than pronotum. Color somewhat variable, from mostly black, except antennae, apical half of rostrum, fore and middle tibiae and tarsi, bases of fore and middle femora, hind tarsi and apex of tibia pale yellowish brown to black with all of legs yellowish except distal $\frac{1}{3}$ of femora dark brown; semi-erect white pectinate setae in small tufts at posterior angles of pronotum, and in large spot along suture behind scutellum; recumbent white pectinate setae on apical margins of elytra and very sparsely scattered on disk, on sides of pronotum, on metepisterna and sides of metasterna, and abdominal segments 2–4, and basal $\frac{2}{3}$ of hind femora; simple erect white setae on pygidium and basal $\frac{2}{3}$ of hind femora; coarse simple erect dark setae on pronotum, elytra, distal half of hind femora and hind tibiae. Figure 2.

Pronotum sparsely punctate on disk, with oval impunctate area along midline slightly behind middle, shining; scutellum inconspicuous. Elytra coarsely punctate, punctures slightly larger than intervals, even intervals raised. Mesosternum vertical, transverse, smooth. Abdomen sparsely punctate on segments 1 and 2. Hind femora relatively short and stout, somewhat swollen with a short acute tooth on inner side at apical $\frac{2}{3}$; hind tibiae terete and slightly sinuate, twisted outward at tip; segment 3 of tarsi nearly $2\times$ wider than segment 2.

Distribution: Alabama, Florida, Louisiana, Illinois, Texas.

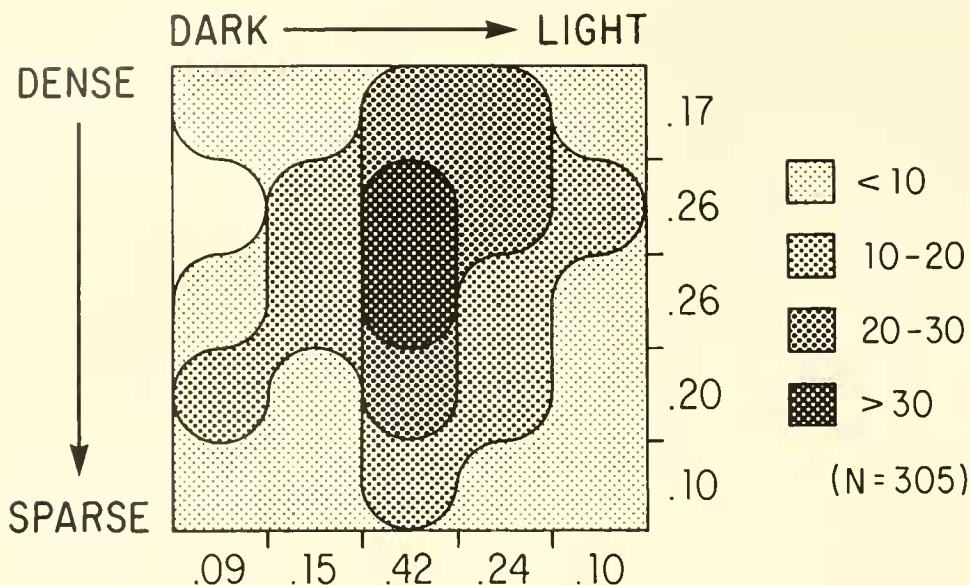


Fig. 8. Relationship between ground color and setation pattern in *Tachygonus lecontei*. Ground color varies from dark to light (Fig. 6); setae vary from dense to sparse. Number of specimens in each category is indicated by shading, and the proportions of all specimens is indicated on the right and bottom margins.

Adult host: *Berchemia scandens* (Hill) K. Koch (Rhamnaceae).

Discussion: Examination of the type of *T. fulvipes* in the collection of the Museum of Comparative Zoology shows it to be teneral, which has probably confused later interpretations of it. My experience in rearing species of *Tachygonus* is that they often emerge from the leaf before becoming completely colored. A specimen from Texas was compared with the types of both *T. minutus* at Purdue University and *fulvipes*, and was found to differ only in color and size. This had been the least frequently collected species of *Tachygonus* in North America until a long series was taken by Robert H. Turnbow in Alabama. These insects were collected on *Berchemia* and differ from the other collections from Louisiana and Texas in having darker legs and being somewhat larger. Because male genitalia were identical and no other consistent differences appear to exist, all are considered conspecific. The distribution of *T. fulvipes* seems primarily to be close to the coast of the Gulf of Mexico, despite the type from "Illinois." The record of Monte (1949) for this species (as *T. minutus*) from Tampico, Mexico, refers to another, undescribed species.

VARIATION IN NORTH AMERICAN *TACHYGONUS*

Because of the variation observed among specimens of *T. lecontei*, *T. tardipes* and *T. rhombus*, these three species were scored for patterns of variation in ground color (*T. tardipes*, Fig. 7), density and color of setae (*T. rhombus*), or both (*T. lecontei*, Figs. 6, 8, 9). Only *T. lecontei* was numerous enough in collections that patterns in variation could be analyzed quantitatively. The following discussion is based on 310 specimens of the species that were assigned to one of five categories of integument color from mostly black to mostly reddish brown (Fig. 6) and one of five categories of densities of setae on the elytra from sparse to dense. Figure 8 shows the relationship between ground color and density of setae for all specimens of *T. lecontei* examined. In general there appears to be a very weak correlation between red coloration and higher density of setae, but most specimens are intermediate in both characters.

Geographic variation in these two characters in *T. lecontei* is shown in Fig. 9. As can be seen, change in the proportions of specimens of different ground color and density of setae changes clinally throughout

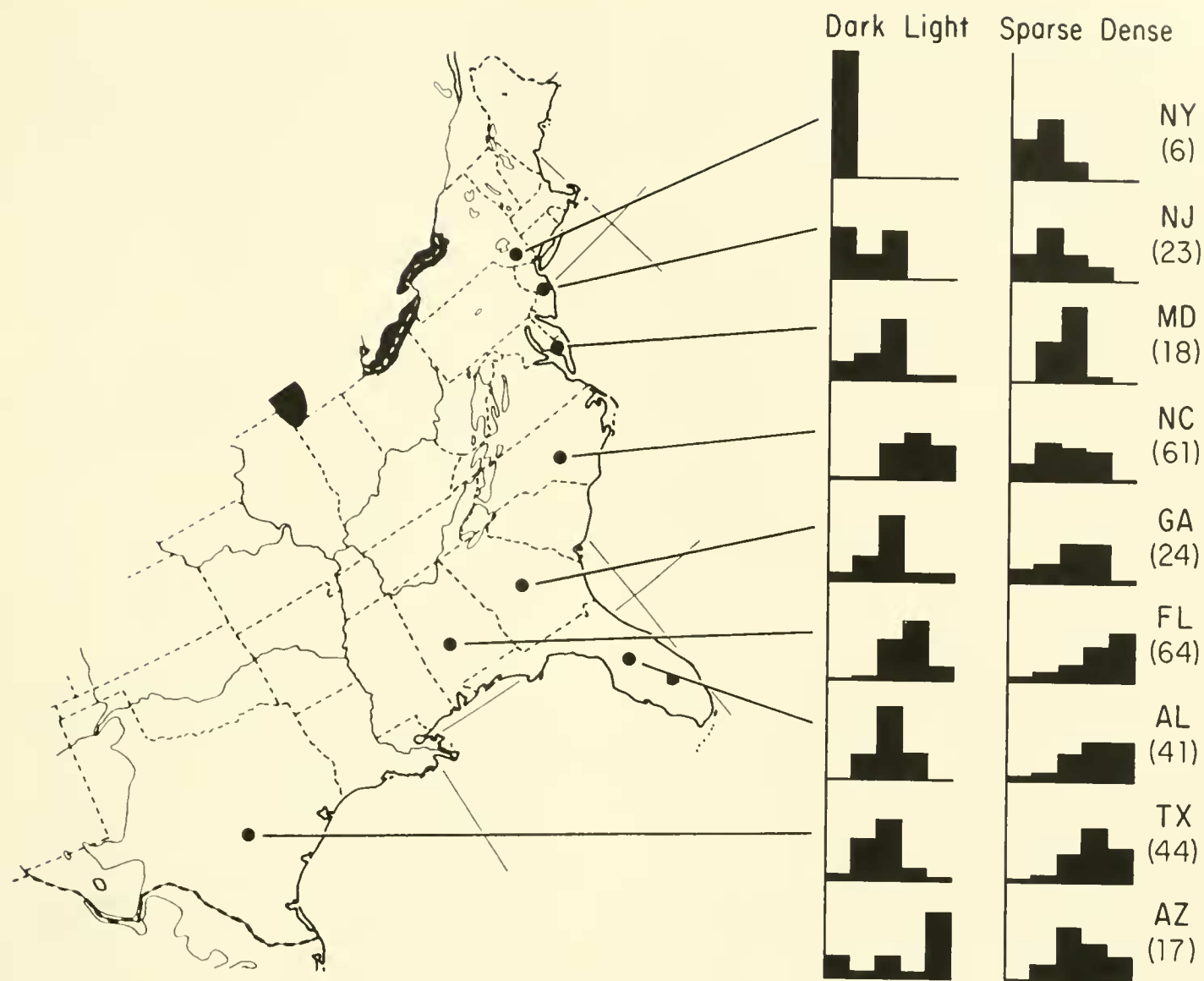


Fig. 9. Geographic variation in ground color (dark to light; Fig. 6) and setation pattern (dense to sparse) for *Tachygonus lecontei* Gyll. Sample sizes for each state given in parentheses.

the range of *T. lecontei*. At the northeastern extreme of the range, New York populations are largely black with relatively sparse setae (“spinipes” form). As one moves south along the Atlantic coastal states, the proportion of individuals that are red and more densely covered with setae increases. Populations increase in the proportions of blacker, less densely covered forms west of Florida. The patterns of variation shown in Fig. 9 must be considered a crude approximation, because specimens were unevenly collected geographically. Systematic sampling and comparison with ecological variables may allow understanding of causal factors.

The pattern of variation becomes more difficult to interpret in Arizona. Although there are only a small number of collections of *T. lecontei* from Arizona, morphs appear to be more distinct and consistent, with relatively few intermediates (Fig. 9). On the other hand, there seems to be no genitalic differentiation between morphs that might suggest separate species, although no males are known from the most distinctive all-red morph. Other characters also vary, however; for example, the hind tibiae are typically rather sharply angulate on the external margin, but are more regularly arcuate in some specimens from Arizona. This more complicated pattern of morphological vari-

ation clearly needs further study, including possible correlation with larval hosts and biology. It is also not clear how or whether the Arizona populations are connected with those in central Texas. There is a complex of forms in Mexico that are either conspecific with or closely related to *T. lecontei* (e.g. *T. nigrocristatus* Champion), some of which have been collected as adults on oak. At present, therefore, it seems most practical to consider all of the Arizona forms under the name of *lecontei* until more extensive and detailed studies are undertaken. Moreover, the large amount of variation in three of North America's five species argues for caution in recognizing new taxa within the genus in general.

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